CORTICAL DEVELOPMENT IN *CHALONERIA CORMOSA* (ISOETALES), AND THE BIOLOGICAL DERIVATION OF COMPRESSED LYCOPHYTE DECORTICATION TAXA

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ABSTRACT. Several anatomically preserved stem fragments showing a wide range of surface features have been discovered among specimens of the Upper Pennsylvanian isoetalean *Chaloneria cormosa*. A comparison of the specimens demonstrates that stems produced a narrow zone of periderm, and that tissues external to the periderm accounted for a moderate increase in stem circumference by two distinctive modes of cell divisions. Depending on the presence or absence of secondary cortical tissues, on differential taphonomy, and on the level at which the cortex is exposed, the surface of a specimen may be comparable to one of several distinctive decortication morphotypes. The outer surface is similar to *Bothrodendron* and *Cyclostigma*, while specimens with leaf bases removed are reminiscent of *Stigmaria*. When fractured through the periderm a *Knorria* surface is produced, while secondary cortical features immediately external to the periderm conform to *Asolanus*. Specimens reveal the anatomical bases for decortication morphotypes and demonstrate that such genera are produced by members of Isoetales as well as Lepidodendrales.

OUR current understanding of Carboniferous vegetation relies upon plant remains that are preserved by several different modes, including compression/impression, cellular permineralization, and mold/cast (Schopf 1975). Upper Carboniferous and Pennsylvanian fossils of varying preservational types typically exhibit differential suites of characters, and traditionally have been studied independently of one another. As a result, a great deal is known about fossils within each group, but remains preserved by different modes seldom have been correlated with the precision necessary to demonstrate whether they represent the same or different taxonomic species.

One group in which correlations of this type are of particular value is Carboniferous Lycopsida. Large Palaeozoic lycophytes produced massive amounts of cortical tissue. Fractured at different surface and subsurface levels, stems typically display characteristic, widely differing features (Renault and Zeiller 1888; Weiss and Sterzel 1893; Thomas and Watson 1976). When preserved as compressions, such morphotypes (DiMichele 1983) are given generic rank but their mode of production, anatomical origin, and biological significance remain poorly understood. Among the most prominent genera are *Asolanus* Wood (1860) and *Knorria* Sternberg (1825). Although *Asolanus* has been described from numerous localities throughout North America, Europe, and Northern Africa (White 1899; Janssen 1940; Crookall 1964; Daber and Kahlert 1970; Lejal-Nicol 1972; Boersma 1978), and is a common component of many compression floras from the Appalachian Basin (Darrah 1969), it is understood only as a characteristic configuration on the rock surface. Through the years it has been described as, or confused with, such diverse structural forms as *Lepidodendron*, *Sigillaria*, *Sigillarioides*, *Pseudosigillaria*, and *Stigmaria* (Crookall 1964). It also has been interpreted as a decortication layer of numerous Carboniferous compression genera (e.g. Daber and Kahlert 1970), or as the outer surface of an otherwise unknown lycophyte stem (White 1899; Janssen 1940). In contrast, *Knorria* is known to represent a decortication surface of lepidodendralean stem genera (Solms-Laubach 1891; Thomas and Watson 1976).

Several additional taxa of Carboniferous lycophyte stem compressions exhibit features unlike those of typical lepidodendrid taxa. The genus *Bothrodendron* Lindley and Hutton (1833) originally was

described as a Carboniferous stem compression with tiny leaf scars and conspicuous halonial branch scars, but it now includes several diverse forms which undoubtedly represent more than one genus of plants. Morphotypes such as *Bothrodendron*, *Pinakodendron* (Weiss and Sterzel 1893), and some species of *Cyclostigma* Haughton (1859) are delimited by overlapping taxonomic criteria. All are characterized by rounded or lenticular leaf scars (or leaf bases) borne in a low helix and widely separated on the stem surface (Crookall 1964). Despite detailed studies of some features (e.g. cuticle and compression surfaces; Thomas 1967), anatomical features of these taxa are poorly known. Consequently, the whole plants represented by Upper Carboniferous specimens of such taxa remain poorly understood (Crookall 1964; Stubblefield and Rothwell 1981).

During the recent study of a new family of Pennsylvanian lycophytes, the Chaloneriaceae Pigg and Rothwell (1983b), several permineralized stems of *Chaloneria cormosa* were revealed on split coal-ball surfaces. Some were exposed at the outer surface of the stem (figs. 21, 22, of Pigg and Rothwell 1983a) with intact leaf bases, epidermis, and cuticle, while others were split at a variety of subsurface levels. The specimens display a wide array of configurations that are very distinct from one another. When compared to compression-impression taxa, they are similar to a variety of genera including *Cyclostigma*, *Pinakodendron*, *Bothrodendron*, *Stigmaria*, *Asolanus*, and *Knorria*. Because the histology and ontogeny of *Chaloneria* are well known, it is now possible to determine anatomical, taphonomic, and ontogenetic bases for the surface configurations that delimit several morphotypes of decortication compression taxa, and to relate more precisely these to the types of plants by which they were produced.

METHODS AND MATERIALS

Specimens of *C. cormosa* are preserved by calcareous cellular permineralization in coal balls from the Duquesne coal (Upper Pennsylvanian) where it outcrops in a roadcut on Ohio State Route 22, approximately 8 km west of Steubenville, Ohio, USA (Rothwell 1976). Surfaces were etched in 5% HCl for 30 sec. to increase contrast for photography. Some coal balls were cut perpendicular to the stem surface and peeled to determine the exact level at which the cortical tissue had split. Other specimens were peeled parallel to the stem surface to identify the anatomical basis for the surface features. Peels were mounted on microscope slides for photography.

Compression specimens of *A. camptotaenia* and cf. *Bothrodendron* photographed for comparative purposes were collected from two Middle Pennsylvanian localities in eastern Ohio. The first is Dorr Run located approximately 1·7 km northwest of Nelsonville (NE $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 30, Wayne Twp., Nelsonville 7·5 min. Quadrangle), Athens Co., Ohio. Stratigraphically these specimens occur in the Snow Fork shale below the Middle Kittanning coal, Middle Kittanning cyclothem, Allegheny Group. The second locality is a strip mine operated by the James Bros. Coal Co., at Mineral City (South centre, Sec. 26, Rose Twp., 7·5 min. Quadrangle), Carroll Co., Ohio. At this locality, fossils are preserved in the shale over the Lower Kittanning (Ohio no. 5 coal), Lawrence–Lower Kittanning cyclothem, Allegheny Group. Pertinent specimens and slides are housed in the Paleobotanical Herbarium, Department of Botany, Ohio University, where they bear acquisition numbers 584, 3375, 3825, 7640–7662.

DESCRIPTION

Surface Morphologies. *C. cormosa* is an Upper Pensylvanian member of Isoetales characterized by a cormose base and an unbranched stem bearing helically arranged leaves (Pigg and Rothwell 1983a, b). Unlike typical members of Lepidodendrales that often have abutting leaf cushions prior to periderm development, the leaf bases of *Chaloneria* are separated by wide areas of stem surface (Pl. 64, fig. 1). Also unlike the leaf cushions of Lepidodendrales, *Chaloneria* leaf bases have irregularly shaped scars where the leaves become detached.

Coal-ball specimens fractured at the outer surface of the stem are characterized by helically arranged leaf bases, about 8–10 mm wide and 5 mm high separated from one another by wide areas of stem surface (Pl. 64, fig. 1; text-fig. 1A). In this regard, *Chaloneria* is similar to several other taxa (e.g. *Bothrodendron*, *Cyclostigma*; Crookall, 1964) that typically lack abutting leaf cushions (Pl. 64, figs. 6, 7; Jennings 1979). Leaf bases of *Chaloneria* have blunt lateral wings, a rounded keel, and either an

apical notch or a ligule pit (Pl. 64, figs. 1, 2). They are also somewhat bulbous, bulging out from the stem surface (Pl. 64, fig. 2), and in this regard are similar to the leaf scars popularly attributed to *Asolanus* (Crookall 1964; Darrah 1969). Distally the leaves of *Chaloneria* abruptly become much narrower (Pigg and Rothwell 1983a). No distal portions of leaves were present on fractured surfaces. When a leaf is detached at a single level the base displays either one or two vascular strands. More frequently, leaves are broken off unevenly, resulting in irregular appearing bases (Pl. 64, fig. 1) in which vascular strands are obscured. There is no evidence of an abscission zone that would provide for the production of regular scars like those on the leaf cushions of Lepidodendrales. Dark, longitudinal strips of tissue are often present on the interfoliar stem surface (Pl. 64, fig. 1), and these represent strips of epidermis and cuticle.
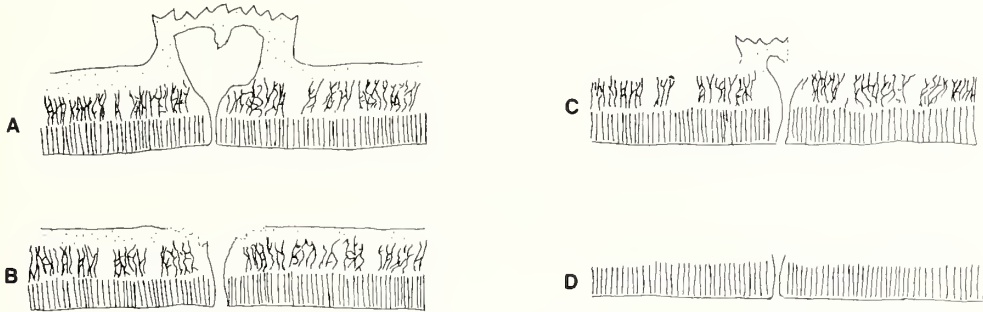
TEXT-FIG. 1A–D. Diagrams of cortical tissues in stems of *Chaloneria cormosa* that have significant periderm; stippled area includes outer cortex in which randomly oriented internal cell divisions occur; distorted lines indicate level at which *Asolanus*-pattern is produced; straight lines indicate periderm. Outer surface of A will appear as *Chaloneria* unless pattern of distorted cortex is impressed on surface, in which case specimen will be recognized as *Asolanus*. Outer surface of B will resemble *Stigmaria* unless pattern of distorted cortex is impressed on surface, in which case specimen will be recognized as *Asolanus*. Outer surface of C has been split at level where regardless of whether leaf bases are detached above (at left) or at interfoliar surface, specimen will exhibit *Asolanus* configuration. Cortex in D has been split at level of periderm such that both inner and outer surfaces will produce *Knorria* pattern.

In other specimens the epidermis is intact in interfoliar areas, but leaves have broken off near or below the stem surface (Pl. 64, fig. 5; text-fig. 1B). In some specimens of this type the interfoliar surface is smooth. On others there are vertically oriented, undulating striations (Pl. 64, fig. 5 at arrows) that conform to the subsurface primary cortical tissue as seen in tangential section (Pl. 64, fig. 3). The most conspicuous features of many specimens are the prominent circular or elliptical parichnos strands that accompany the leaf traces (Pl. 64, fig. 3). They are similar to appendage scars on stigmarian axes, with the rounded parichnos strands of *Chaloneria* (Pl. 64, fig. 5) corresponding to the aerenchymatous middle cortex of stigmarian appendages. There is a further resemblance with *Cyclostigma*, which in the past also has been confused with *Stigmaria* (Crookall 1964).

Two additional cortical patterns of *Chaloneria* are commonly represented on split coal-ball surfaces. Several specimens are characterized by an anastomosing pattern of diagonal striations (text-figs. 1C, 2a, b). Of these, some exhibit bulbous leaf base scars (text-fig. 2b), while in others the leaf base is broken off at a more proximal level, revealing axially elongate rather than rounded parichnos strands (text-fig. 2a). This pattern conforms to the compression taxon *Asolanus* (Wood 1860) based on the characteristic interfoliar pattern (Pl. 64, fig. 8; text-fig. 2a, b).

An additional, commonly preserved surface of *Chaloneria* cortex is characterized by densely compact cells (text-fig. 2e, g) and lacks striations or other prominent interfoliar features (text-figs. 1D,

2*e*). Specimens of that type each possess a vascular strand that is surrounded by an oval or vertically elongate, lenticular parichnos strand (text-fig. 2*e*). This type of decortication pattern is comparable to *Knorria* (Sternberg 1825).

Anatomical origin of surface features. In transverse section an immature specimen of *Chaloneria* exhibits a medullated protostele surrounded by primary cortical tissues; this pattern is also present in distal stem regions (Pigg and Rothwell 1983*a*). Most stems are flattened (Pl. 64, fig. 4), lacking preserved pith and inner cortex. In the inner zone of commonly preserved primary cortex the cells possess differentially thickened walls and frequently broken tangential walls (Pl. 64, fig. 4 at top). This results in a resemblance to distorted radial rows of periderm (Pigg and Rothwell 1979). Tangential sections through the zone (Pl. 64, fig. 3) reveal the undulating, vertically oriented pattern that is sometimes present on the epidermis (Pl. 64, fig. 5 at arrows). This pattern is also characteristic of the interfoliar region on the stems of many compressions, where it is interpreted as the result of distortion during diagenesis (Pl. 64, fig. 7; Rex and Chaloner 1983).

Older and more proximal stem segments exhibit secondary cortical tissues that are derived both from a continuous cambium (viz. periderm) and from the internal subdivision of individual cortical cells (Pl. 64, fig. 2). Periderm is represented by a zone of radially aligned cells with differentially thickened radial walls, and is present along the inside of the commonly preserved cortex (Pl. 64, fig. 2). In stems with little periderm (Pl. 64, figs. 4, 5) the primary cortex and epidermis remain relatively intact and unaltered. In stems with larger amounts of periderm the epidermis and cuticle are separated into longitudinally oriented strips of tissue at the periphery of the stem (Pl. 64, fig. 1). In these specimens, cortex outside the periderm appears distorted (Pl. 64, fig. 2 at sides; text-fig. 1A–C). Tangential sections of the tissue reveal narrow, vertically elongated lenticular regions where the cells are laterally expanded, and in which some internal cell divisions have occurred (text-fig. 2*f*). These regions alternate with areas of narrow primary cortical cells (text-fig. 2*d*,*f*). The alternation of these zones produces a pattern of discontinuous light and dark strips (text-fig. 2*c*) in specimens with little periderm (e.g. Pl. 64, fig. 4). Stems with a thicker zone of periderm (e.g. Pl. 64, fig. 2) have a distinctive pattern of diagonal lines in the interfoliar region. When seen on split surfaces this pattern produces the *Asolanus* configuration (text-fig. 2*a*, *b*). Cortical growth of this type undoubtedly could accommodate only a moderate increase in circumference of the stem, and this is consistent with the periderm of *Chaloneria* being up to only about 2 mm thick (Pl. 64, fig. 2). Expansion of the subepidermal cortex is accomplished by the randomly oriented subdivision of many cells (Pl. 64, fig. 2 at arrow), another

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EXPLANATION OF PLATE 64

Figs. 1–5. *Chaloneria cormosa.* d, distorted cortex; p, parichnos; pc, primary cortex; pe, periderm; s, stele. 1, surface view of stem in which secondary growth has split epidermis into longitudinally oriented strips, O.U.P.H. no. 3825, × 1. 2, transverse section of cortex showing leaf base and interfoliar region after significant secondary growth. Arrow indicates position of outer cortex in which randomly oriented internal cell divisions have occurred, C.B. 1399A top no. 9, × 7. 3, tangential section near surface of stem with only primary growth. Primary cortex exposed at centre and leaf bases sectioned at sides, C.B. 1398D(1) side no. 310, × 2·5. 4, transverse section of flattened stem with little periderm. Outer surface of cortex at top comparable to that in fig. 5, outer surface of cortex at bottom comparable to that in text-fig. 2*c*. C.B. 2126A bottom × 7. 5, surface view of stem with leaf bases broken off at level of interfoliar stem surface and intact epidermis. Note vertically undulating, longitudinal pattern (at arrows) that conforms to cellular pattern of primary cortex in fig. 3, C.B. 2127A(2), × 1.

Fig. 6. *Bothrodendron*-type impression of stem surface with relatively smooth interfoliar surface. O.U.P.H. no. 7642, × 2·5.

Fig. 7. *Bothrodendron*-type impression of stem surface with longitudinally oriented, vertical pattern similar to that of primary cortex in *Chaloneria*, O.U.P.H. no. 7643, × 2·5.

Fig. 8. *Asolanus* impression of stem with leaf bases similar to those in figs. 6 and 7, and interfoliar pattern similar to that of *Chaloneria* specimens in text-fig. 2*a*, *b*. O.U.P.H. no. 7644, × 1.
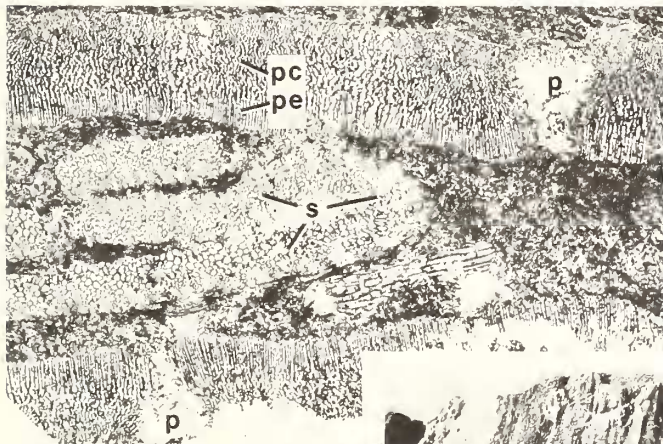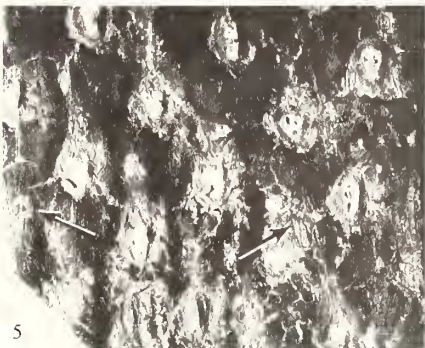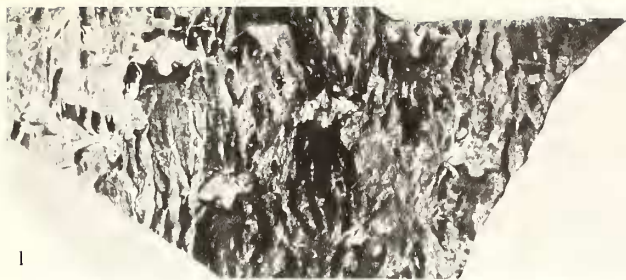
PLATE 64

PIGG and ROTHWELL, Carboniferous *Chaloneria* (*Isoetales*)
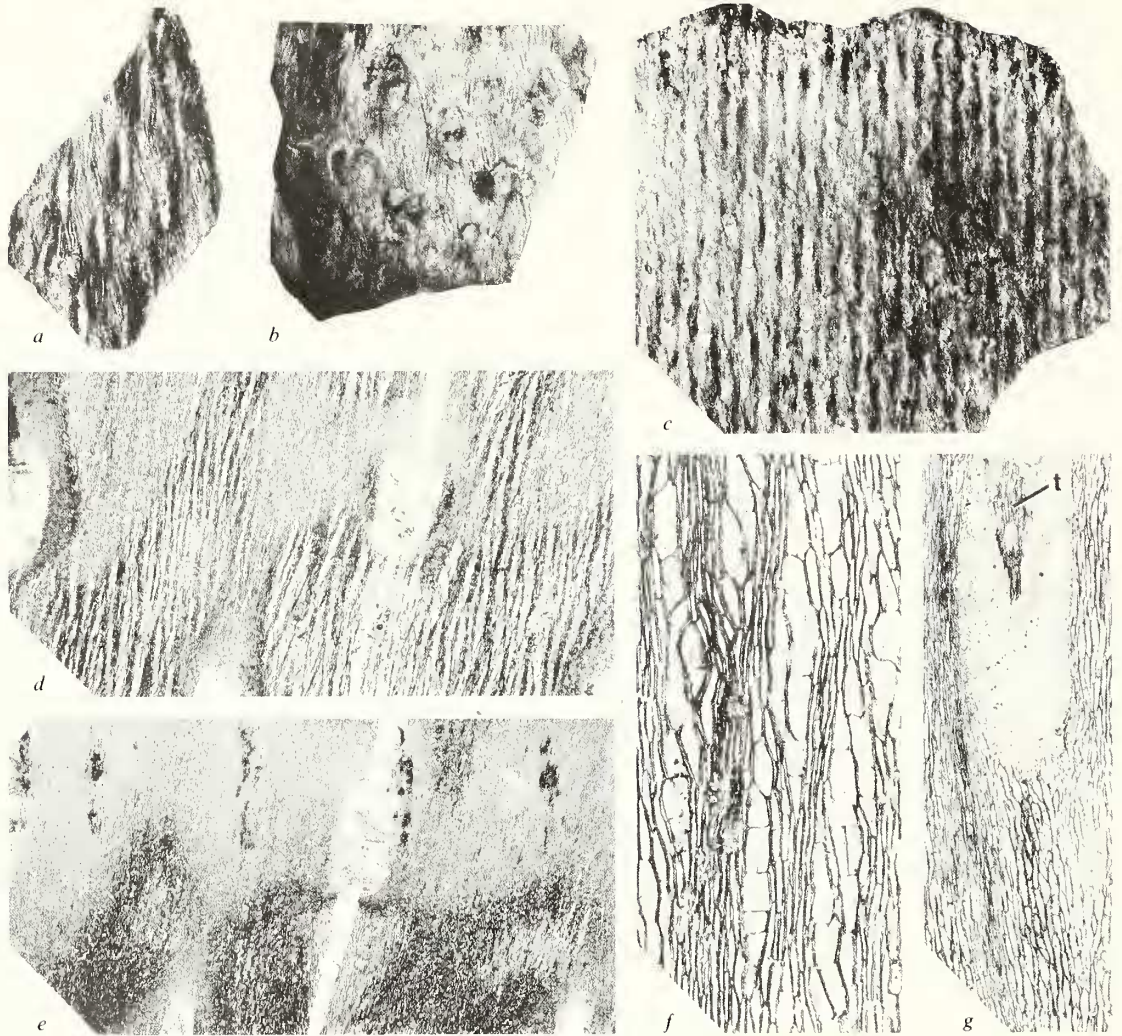
TEXT-FIG. 2a–g. *Chaloneria cormosa* cortex in surface views and in tangential sections; t, leaf trace. *a*, cortex of specimen with well-developed periderm, split at level of 'd' in Plate 64, fig. 2, C.B. 2126, × 1. *b*, cortex of same specimen as *a*, but with leaf bases split slightly further toward periphery, at level comparable to specimen in Plate 64, fig. 5, C.B. 2126, × 1. *c*, surface of cortex at level similar to that in Plate 64, fig. 1, but from specimen with only limited periderm, comparable to outer surface of cortex at bottom of Plate 64, fig. 4, C.B. 2126, × 1. *d*, tangential section through cortex of specimen with significant periderm, comparable to surface in *b*, C.B. 2127A(1) Side no. 6, × 2·5. *e*, tangential section through periderm of specimen in D showing anatomical derivation of *Knorria* configuration, C.B. 2127A(1) side no. 9, × 2·5. *f*, enlargement of anatomical detail in *d*, C.B. 2127 no. 7, × 17. *g*, enlargement showing anatomical detail of tissue that compresses to produce *Knorria* configuration, C.B. 1398D(1) side no. 310, × 17.

indication of only limited increase in girth due to secondary growth. The interfoliar pattern similar to *Asolanus* commonly found among specimens of *Bothrodendron*, *Cyclostigma*, and *Pinakodendron* is consistent with the interpretation that they also had limited periderm production, and a cortical zone that became distorted by secondary growth similar to that in *Chaloneria*. If some species of these

genera represent small trees, as supposed by some authors, then the majority of the ultimate stem diameter must have been produced by primary growth.

Tangential sections or fractures through the periderm of *Chaloneria* reveal homogeneous tissue traversed by leaf traces and accompanying parichnos (text-figs. 1D, 2e, g), and produce a *Knorria* configuration (text-fig. 2e). The occurrence of *Knorria* in association with many lepidodendrid specimens probably also represents tangential sections through the periderm. Considering the massive amounts of periderm they produced, it is not surprising that *Knorria* is of such common occurrence among lepidodendrids. However, because smaller forms such as *Chaloneria* also produced periderm, *Knorria* should be expected to occur among specimens of them as well.

DISCUSSION

Plant Size Estimation. Because the broad inner cortical region and pith are rarely present in anatomically preserved stems of *Chaloneria*, specimens are almost always represented by a highly flattened cylinder (DiMichele *et al.* 1979; Pigg and Rothwell 1983a) that must have collapsed quite early during diagenesis. Under these circumstances, instead of the width of the flattened *Chaloneria* stems being a rough approximation of their diameter in life (as proposed in the compression model of Walton 1936; Rex and Chaloner 1983), it was probably exaggerated significantly. A more realistic approximation of the original diameter of the flattened stems is obtained by considering their width to represent one-half the circumference. In such a case the original diameter can be calculated by doubling the width of the stem, and considering that figure to represent the original circumference. The stem diameter is then easily calculated by considering circumference (C) to be equal to πD, where D = stem diameter. If this interpretation of the taphonomic alteration of stems is correct, then the size of compressed plants with a similar mode of cortical growth (e.g. as in *Asolanus*) may have been overestimated by many previous authors.

Developmental Interpretation. Some stems of *C. cormosa* exhibit only primary growth, and in these axes the preserved cortical tissues are relatively homogeneous (Pl. 64, fig. 3 at centre). Variations from specimen to specimen are due primarily to taphonomic processes including uneven leaf detachment, differential preservation, dissimilar amounts of crushing, and the impression of subsurface cortical patterns (Pl. 64, fig. 3) on to the epidermis (Pl. 64, fig. 5; Rex and Chaloner 1983). The cortex in specimens of this type lacks regions of anastomosing cells and radially aligned cells.

By contrast the onset of secondary growth produced several distinctive layers of cortical tissues. The most regular of these is the zone of radially aligned peridermal cells that are located at the inner margin of the commonly preserved cortex. This is also the zone that initiated an increase in the girth of the stem. In stems with prominent periderm, lenticular areas that are characterized by internally septate cells developed to the periphery of the periderm (Pl. 64, fig. 2; text-fig. 2d). Such areas represent a mechanism for maintaining tissue continuity immediately outside the periderm during the increase in girth. It is clear that many cells in the outermost cortex also remained meristematic at the onset of periderm production, such that the longitudinal fissures on the stem surface are restricted primarily to the epidermis. However, the outermost zone of cortical cells grew by more random patterns of internal cell divisions (Pigg and Rothwell 1983a).

Systematic Implications. Documentation among specimens of *C. cormosa* of the anatomical and taphonomic features that produce several morphotypes of lycophyte stem surface patterns provides a basis for relating such morphotypes to a diverse assemblage of Palaeozoic plants. It also provides evidence for the modes of cortical development in compression/impression forms that previously have been known primarily as surface patterns. In taxa of compressed stems with distantly spaced leaf bases such as *Bothrodendron, Cyclostigma*, and *Pinakodendron*, a relatively smooth interfoliar region (Pl. 64, fig. 6) probably displays a less distorted outer surface than specimens with characteristic interfoliar patterns (Pl. 64, figs. 7, 8; Rex and Chaloner 1983). Among the latter specimens, those with gently undulating patterns (Pl. 64, fig. 7) show features similar to those of the primary cortex in *Chaloneria*, and were undoubtedly preserved prior to, or distal to, secondary cortical development. In contrast,

stems with the *Asolanus*-type diagonal interfoliar pattern (Pl. 64, fig. 8) reveal that significant secondary cortical activity like that of *Chaloneria* had occurred prior to fossilization. Some specimens of this type represent decortication external to the periderm (text-fig. 2*a*, *b*), while others have had the subepidermal configuration impressed on the outer surface of the stem (text-fig. 2*e*). As emphasized by Rex and Chaloner (1983) specimens of the latter type may show both surface and subsurface features at the same level. This accounts for the occurrence of external leaf-base scars that are separated by a subsurface *Asolanus*-type cortical pattern on some specimens (Pl. 64, fig. 8). While isoetaleans like *Chaloneria* were probably the most common source of such decortication surfaces, some lepidoden-draleans with relatively moderate secondary development (e.g. *Lepidodendron dicentricum*, Eggert 1961) produced 'phellem meshes' that may appear similar to *Asolanus* when seen on a split surface. The specimens of *Asolanus* interpreted as a *Lepidodendron* by Daber and Kahlert (1970) could reflect this mode of growth.

It is now clear that the *Knorria* pattern is produced when the cortex is split through or at the surface of the periderm in both Lepidodendrales and Isoetales, and that its more common occurrence with lepidodendraleans is probably the result of the much more massive periderm produced by the group. Likewise, the *Asolanus* configuration results from either decortication peripheral to the periderm or from the imprinting of subsurface features on the epidermis in plants with the capacity for only limited periderm production after much of the secondary cortical production had been completed.

Through continuing efforts to determine the biological and taphonomic origins of compression features (e.g. Rex and Chaloner 1983) and the anatomical basis for morphological features, the significance of many lycophyte morphotypes is becoming increasingly clear. In terms of both taxonomic significance and ontogenetic potential the increased knowledge allows for a better understanding of lycophyte evolution, and provides the basis for more accurate interpretations of remains preserved as coalified compressions or impressions.

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